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Studies on Loricate Ciliophora II. *Folliculina boltoni* Kent

By JOHN MEACHAM HAMILTON

The family Folliculinidae is composed of ciliated Protozoa which belong to the order Spirotrichida. The family is characterized by a flask-shaped, transparent lorica and by a peristomial field drawn out into two wing-like projections which can be extended beyond the aperature of the lorica when the animal is feeding, and can be withdrawn into the lorica when the animal contracts. The known species of this family are all marine except for one fresh water form, *Folliculina boltoni.* This unique member of the family has been found in Europe and South America, and Wailes (1928) described it from a fresh water lake on Vancouver Island, B. C., but Andrews (1948) considers this record to be questionable. The occurrence of *F. boltoni* in Iowa has been reported by the author (Hamilton, 1950a).

Penard (1919) and Thomsen (1921) have studied the morphology of *F. boltoni* and the former observed some stages in the life cycle. Apparently, however, observations on the migratory stages of this animal have been fragmentary. Kahl (1935) and Fauré-Fremiet (1936) suggest that the marine form, *Folliculina simplex* is morphologically identical to *F. boltoni.* The morphology and life cycle of *F. simplex* have been given by Fauré-Fremiet (1932) who provisionally identified the species as *F. ampulla,* but later (Fauré Fremiet, 1936) he states that the animal was *Folliculina simplex.*

HABITAT

Specimens of *Folliculina boltoni* were obtained from Lake Okoboji, Dickinson Co., Iowa, on glass microscope slides which were suspended in pairs in wooden racks in the water near the dock at the Iowa Lakeside Laboratory. The margin of the lake at this point has a sandy bottom with a heavy growth of aquatic plants (*Potamogeton, Vallisneria, Myriophyllum,* and *Ceratophyllum*) up to within two to three meters of the edge of the water. At the shore line, there are glacial rocks which have been deposited by the action of the ice during the winter. These range in size from coarse gravel up to about half a meter in diameter. The submerged portion of the rocks is covered by periphyton consisting of algae, sponges, bryozoans, and a large number of other organisms.

The slides which yielded the specimens of *Folliculina* were submerged in racks very near the rocks at the shore line, and also at a depth of about two meters in the vegetation at the end of the dock, about ten meters from the shore. The folliculinids usually became attached to the lower surface of the pairs of slides in these racks.

In one experiment, slides were placed in a gallon jar containing well areated, boiled water and one of the rocks from near the place in the lake where the slides had been submerged. After about a week, during which air was bubbled through the water intermittently, the slides were examined and specimens of Folliculina were among the organisms found. It appears that, in this experiment, the folliculinids must have come from the rock, although previous workers (Kent, 1880/81; Penard, 1919; and Thomsen, 1921) report *Folliculina boltoni* as being found on plants.

Morphology

The flask-shaped lorica ranges from 170 to 200 microns long, 130 to 160 microns wide, and 40 to 70 microns high. It is less than one micron thick and is either colorless or slightly tinged with greenish-blue pigment. No chestnut-brown specimens such as those described by Kent (1880/81) were observed. Also it was not possible to find internal valves in the neck of the lorica, although Thomsen (1921) describes such structures in this species.

The animal is broadly attached to the base (*i. e.*, that part farthest from the aperture) of the lorica (Fig. 2) as described by Thomsen (1921), not by a rounded point as shown by Penard (1919) in his figures. When contracted, the organism is semicircular at the basal end, and the distal end terminates asymmetrically in a blunt point (Fig. 1.). This point is usually on the observer's left (when the animal is viewed from the side opposite the attachment of the lorica and with the base of the animal toward the observer), while to the right of the apex lies the concave vestibule, bearing the adoral zone of membranelles as a band around the edge and extending as a spiral to the bottom of the cavity.

When fully extended, the peristome protrudes through the aperature of the lorica and spreads out like a funnel with two flap-like projections, unequal in size, which are connected on one side by a broadly rounded edge and on the other by a deeper, more abrupt, notch (Fig. 2). Kent (1881/82) states that the left lobe is usually the larger. Penard (1919) indicates that the larger lobe is sometimes on the right and sometimes on the left, while Thomsen (1921) says that the right wing (in ventral view [?]) is usually the larger, but that the neck is very flexible and may turn in any direction. Study of the specimens from Iowa shows that the larger lobe arises from the distal tip of the contracted animal, and as stated above, that this pointed structure is usually on the observer's left. How-

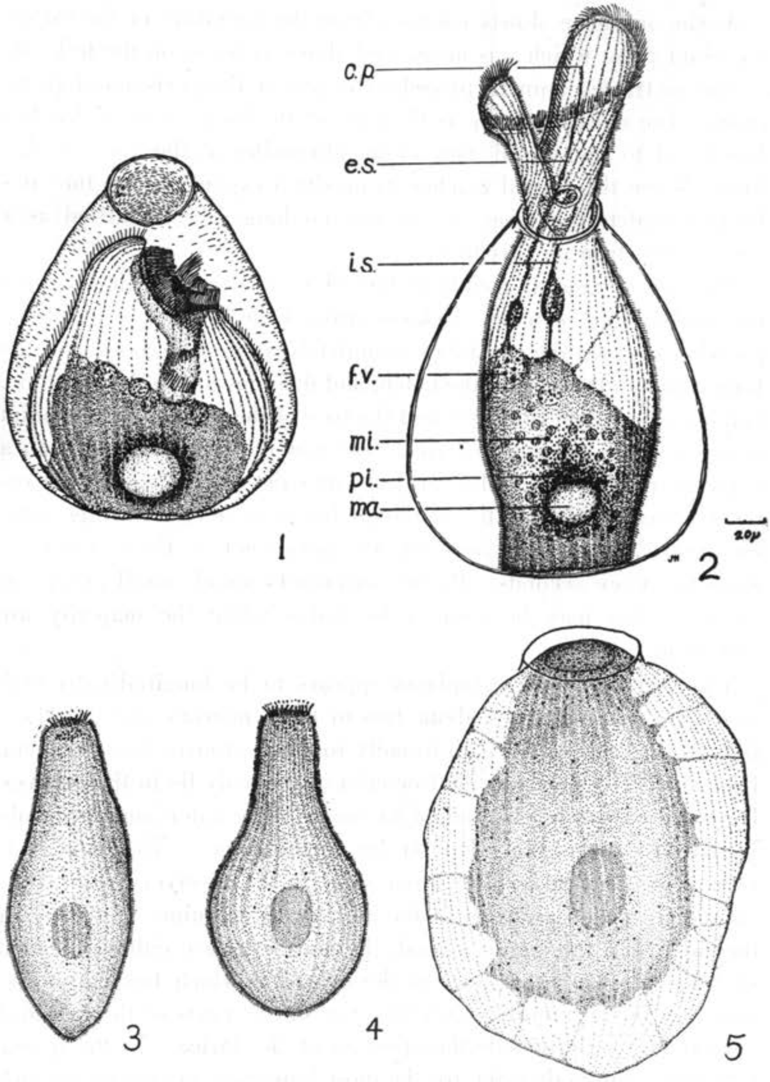

Fig. 1. Sessile *Folliculina boltoni*, contracted within its lorica.
Fig. 2. Sessile individual, fully extended. *c. p.*, cytopyge; *e. s.*, egestion strand; *f. v.*, food vacuole; *i. s.*, ingestion strand; *ma.*, macronucleus; *mi.*, micronucleus; *pi.*, pigment granules.
Figs. 3, 4. Migratory individuals showing two forms taken while swimming.
Fig. 5. Early stage in the metamorphosis of a migratory to a sessile form with the neck of the lorica just started.

ever, the extended neck is flexible and may be turned as shown (Fig. 2), but when it is twisted, the lines of body cilia show this fact clearly. When the larger lobe is on the left, the notch is on the side away from the observer; when the larger lobe is on the right, the notch is on the side toward the observer.

As the organism slowly emerges from the aperature of the lorica, the blunt point which was mentioned above as being on the left side of the contracted animal, precedes the rest of the peristomial structures. The most distal tip is the part of the larger lobe which lies just basal to the adoral zone of membranelles at the apex of this lobe. When the animal reaches its maximal expansion, the lobe unfolds completely so that the tip can no longer be identified as a special structure on this lobe.

The row of adoral membranelles (Fig. 2) starts at the apex of the smaller lobe, extends clockwise around the broadly rounded depression between the two lobes, completely around the border of the larger lobe to the base of the notch, and then down into the vestibule, making a complete spiral around the base of the vestibule at the point where it enters the cytopharynx. The row of membranelles is on a ridge of protoplasm which projects into the vestibule. In the extended, feeding animal, the membranelles may be seen beating metachronously. At times, however, the movement of these structures stops for a few seconds. In the contracted animal, small groups of membranelles may be seen to be active while the majority are quiescent.

The surface of the cytoplasm appears to be longitudinally striated with parallel lines about two to three microns apart. These lines are narrow ridges with broadly rounded grooves between them. Penard (1919) says that the fine cilia of the body lie in the grooves. However, in specimens studied by means of a water immersion objective, it appears that the cilia are on the ridges. The basal ends of the cilia seem to be just to one side (to the observer's right when viewed with the basal end of the animal toward him) of the tip of the ridge. In the sessile animal, the body cilia are either quiescent or beat feebly on that part of the organism which lies within the lorica. They are more active, however, on the parts of the extended animal which lie outside the aperture of the lorica. In the migratory stage, the body cilia are the most important organs of locomotion.

The protoplasm in the basal part of the animal is granular with scattered food vacuoles. It is presumed to be highly viscous since brownian movement is not seen in this region and since it retains its shape for some time after the rest of the animal is cytolyzed following death. Within this dense cytoplasm there are blue-green pigment granules which give the organism its characteristic color. The amount of this pigment varies in different individuals.

The distal half of the animal is transparent and appears to be completely free from granules or pigment except for a thin layer of granular cytoplasm which lies around the periphery, and sheets of similar granular material which divide the rest of this part of the organism into large irregular vacuoles (Fig. 2). Most of the granules in the peripheral layer lie under the ridges of the pellicle and move along these ridges, sometimes in one direction and sometimes in the other. Occasionally a granule will be seen to pass under the furrow from one ridge to the one beside it. Penard (1919) and Thomsen (1922) believe that the clear area in the distal part of the animal serves the function of a contractile vacuole. No evidence to confirm this was observed in the course of the present work. Neither was any typical contractile vacuole observed.

Feeding is accomplished by means of the membranelles which sweep particles into the vestibule. Food vacuoles are formed in the cytopharynx at the base of the vestibular cavity. After the food particles have accumulated the vacuole closes off at the vestibular-cytopharyngeal junction, and the spindle-shaped vacuole moves down a permanent, narrow strand of granular cytoplasm which runs through the clear, distal part of the animal to the basal, dense cytoplasm. We shall refer to this strand of granular cytoplasm as the *ingestion strand*. This pathway for food vacuoles is comparable to the "pharyngeal tube" described by Noland and Finley (1931) for *Vorticella* and by the present author (Hamilton, *in preparation*) for *Cothurnia variabilis*. Waste granules and food residues are discharged in vacuoles which pass from the basal dense cytoplasm through a second granular strand an *egestion strand*, which runs to the cytopyge on the outer surface of the middle of the larger peristomial lobe (Fig. 2). The food vacuoles and waste vacuoles are several times the diameter of the ingestion and egestion strands of cytoplasm and these vacuoles seem to move along the strands by a peristaltic-like action.

The macronucleus is ovoid, about thirty microns in diameter, and may be seen in the living animal in the center of the granular cytoplasm. Penard (1919) says that there are three of four micronuclei, but this number is probably too small. There are twelve to fifteen spherical bodies that stain darkly with hematoxylin and are interpreted as micronuclei. They are about two microns in diameter and are scattered in the dense cytoplasm around the macronucleus.

Fission and Migration

Fission was observed in only a few instances, but the process seems to be similar to that which was described by Fauré-Fremiet (1932) for *Folliculina simplex.* A few loricae containing two individuals were observed and in these, one of the organisms usually contained more blue-green pigment than the other. In every case observed, the organism with the greater amount of pigment was the one which mirgated.

When it leaves the lorica, the migratory individual becomes elongated and narrow (Fig. 3), but it soon changes to a bottle shape with a rounded posterior end and a narrow, elongated neck (Fig. 4). The cilia on the surface of the body are arranged in parellel rows as they are in the sessile organism. At the anterior end, there is a ring of membranelles which are about twice as long as the body cilia. These anterior membranelles beat as the organism swims, but as stated above, the body cilia are the most important organs of locomotion in the migratory stage. Just behind the anterior ring of membranelles there is a mass of blue-green pigment like that described by Fauré-Fremiet (1932) for *Folliculina simplex.* From time to time, the swimming organism pulls in its neck and becomes pear shaped, but does not enclose its peristomial membranelles when it contracts.

Lorica Production

One organism was found which apparently had recently come to rest (Fig. 5). It was flattened against the slide with an irregular oval boundary measuring about 165 by 100 microns. Later this animal contracted its margins to about 135 by 90 microns. It is presumed that during the expanded stage a cementing substance was secreted since scattered fine granules were seen to be attached to the slide around the animal after it contracted. A short time later the animal had formed the neck of the lorica but had not, in so far as could be determined, produced any part of the body of the encasement. The animal died before completing its lorica. A similar specimen was found on a slide that had been fixed, stained, and mounted in balsam. The neck of the lorica is clearly visible in this specimen, but there is no indication that the rest of the lorica has been produced.

In the two organisms described above, the dense cytoplasm and nucleus were in the center of the body, while all around the periphery there were a large number of large clear vacuoles (Fig. 5). These vacuoles may have been seen by Penard (1919) who, while discussing the transformation from the motile to the sessile stage, says, "Some minor facts concerning vacuoles or lacunae . . . might be referred to . . .". He does not, however, discuss these vacuoles or show them in his figures. It is suggested that these vacuoles cause the organism to enlarge at the time of lorica formation, and that later some of them are lost and the organism shrinks away from the lorica to assume the adult form. Such vacuoles would be comparable to the *expansion vacuoles* which have been described (Hamilton, 1950b) for *Cothurnia variabilis.*

Later stages in the development of the lorica were not observed due to the scarcity of material and the difficulties in keeping the organisms alive while they were under observation.

Summary

1. Specimens of *Folliculina boltoni* Kent from Lake Okoboji, Iowa, are described.

2. The animals are broadly attached to the base of a flask shaped lorica.

3. When extended, the peristomial wings are unequal in size. Except when there is evidence of twisting, the larger wing is to the observer's left.

4. The cytoplasm is divided into a basal, dense, granular cytoplasm, and a distal, non-granular region. Strands of granular cytoplasm, called *ingestion* and *egestion* strands cross the clear distal region and mark the pathways for food and waste vacuoles.

5. Peristomial mambranelles serve the sessile animal for feeding, while parallel rows of body cilia are the chief locomotor organs of the motile stage.

6. Evidence indicates that immediately after becoming sessile, the animal increases in size by the production of vacuoles; secretes its lorica by producing the neck first, and then the rest of the encasement; and finally loses some of its vacuoles and shrinks away from its lorica.

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